

20.

Comparative Biology of Salticid Spiders at Rancho Grande, Venezuela.
Part V. Postembryological Development of Color and Pattern.¹

JOCELYN CRANE.

Research Zoologist, Department of Tropical Research, New York Zoological Society.

[This is one of a series of papers resulting from the 45th, 46th and 47th Expeditions of the Department of Tropical Research of the New York Zoological Society, made during 1945, 1946 and 1948 under the direction of Dr. William Beebe, with headquarters at Rancho Grande in the National Park of Aragua, Venezuela. The expeditions were made possible through the generous cooperation of the National Government of Venezuela and of the Creole Petroleum Corporation.

[The characteristics of the research area are in brief as follows; Rancho Grande is located in north-central Venezuela (10° 21' N. Lat., 67° 41' W. Long.), 80 kilometers west of Caracas, at an elevation of 1,100 meters in the undisturbed montane rain forest which covers this part of the Caribbean range of the Andes. Adjacent ecological zones include seasonal forest, savanna, thorn woodland, cactus scrub, the fresh-water lake of Valencia and various marine littoral zones. The Rancho Grande area is generally subtropical, being uniformly cool and damp throughout the year because of the prevalence of the mountain cloud cap. The dry season extends from January into April. The average humidity during the expeditions, including parts of both wet and dry seasons, was 92.4%; the average temperature during the same period was 18° C.; the average annual rainfall over a five-year period was 174 cm. The flora is marked by an abundance of mosses, ferns and epiphytes of many kinds, as well as a few gigantic trees. For further details, see Beebe & Crane, *Zoologica*, Vol. 32, No. 5, 1947. Unless otherwise stated, the specimens discussed in the present paper were taken in the montane cloud forest zone, within a radius of one kilometer of Rancho Grande.]

CONTENTS.

	Page
Introduction	253
Historical Review	254
Systematic Account	255
Lyssomaninae	
<i>Lyssomanes bradyaspilus</i>	255
Marpissinae	
<i>Menemerus bivittatus</i>	255
Synagelinae	
<i>Semorina brachychelyne</i>	256
Dendryphantinae	
<i>Ashitaba furcillata</i>	256
<i>Sassacus flavicinctus</i>	257
<i>Sassacus ocellatus</i>	257
Hyllinae	
<i>Phiale</i> spp.	257
Plexippinae	
<i>Corythalia</i> spp.	258
Magoninae	
<i>Mago denticelalis</i>	258
Summary and Conclusions	259
References	261

INTRODUCTION.

This is the fifth of a series of papers dealing with the salticid spiders of Rancho Grande, Venezuela. Part I (Crane, 1948.1) discussed the taxonomy and life histories of three species of *Corythalia*, including post-embryological development; Part II (1948.2) described methods of study; Part III (1949.1) dealt with systematics and behavior in the adults of eight new species and Part IV (1949.2) concerned display. The present paper is restricted to descriptions and comparisons of postembryological development of color and pattern in the same species considered in the previous sections.

Under each species, a résumé is given of the adult appearance; complete descriptions will be found under the type description or other quoted references. Descriptions of the young are given less fully than those of *Corythalia*, which were treated exhaustively in order to determine the range of variation in closely related species. In the present paper, the aim is rather to show general trends of pigment and pattern development in the various groups. To what extent they are metabolic, genetic, adaptive and vestigial remains largely in the realm of speculation; discussion of these theoretical considerations is being reserved until after publication of the remaining sections on post-embryology.

Because of the range of intermediate steps between "hairs" and "scales," and their frequent occurrence in the young, the word "elements" will be used where a general term is needed to cover short, integumentary structures, sometimes called "protective" by earlier writers, and excluding bristles, trichobothria and spines. The standard abbreviations AME, ALE, PME and PLE are employed throughout for the various eyes, antero-medial, antero-lateral, postero-medial and postero-lateral, respectively. The terms "instar" and "stadium" are used interchangeably. The "first instar" corresponds to the "1. *Postembryonalstadium*" of Holm (1941).

Although many other immature individuals were collected, only those young have been included in the material for this paper in which colors were described in life, since fading in alcohol is even more prevalent in the young than in adults. Since few speci-

¹ Contribution No. 886, Department of Tropical Research, New York Zoological Society.

mens were reared throughout the life cycle, the correct instar names could be given only to the early ones, reared from the egg. Hence the terms "pre-pre-penultimate instar," "pre-penultimate instar" and "penultimate instar" are used, respectively, for the third stadium before the adult, the second before the adult and the preadult. These older juveniles were determined by rearing after capture in the half-grown state. Although middle instars, especially the fourth and fifth, are usually missing from the series, all of the species could undoubtedly be reared through the complete cycle, as in *Corythalia*, given sufficient time and care.

In the following descriptions, the black pigmentation of the eye capsules is not mentioned, since in every case this begins development late in the first instar, and is highly developed in the second. This is often supplemented externally by especially dense black pigment in the hypodermis of the eye tubercles, which is particularly conspicuous in those adult females and young having otherwise light-colored carapaces. Also unmentioned are the black tarsal pads and claws which are more or less pigmented from their appearance in the second instar; and the leg spines, which develop pigment gradually and sometimes become very dark by the middle instars, as in the plexippinids.

HISTORICAL REVIEW.

The vivid hues of salticid spiders have been remarked from the days of Wallace and before. As with birds and butterflies, however, the brilliance of a few has given a reputation to the entire group, a majority of which are not, to human eyes, conspicuous even in the adult. As in birds, bright pigments and structural iridescence are rarely found before the approach to maturity.

Very few studies have been made on the development of pigments and patterns in salticids. Wagner (1888, p. 296 ff.), who included salticids in his material, described the histology of tactile hairs during the molting of spiders; deposition of pigment, however, was barely mentioned. Later (pp. 361-362) he dealt with color development in very general terms, noting the frequent similarity of females and young, and the late development of adult male coloration.

The Peckhams occasionally mentioned color patterns of young salticids in connection with their discussions of secondary sexual characteristics and of species differences (1889, pp. 14-25, col. pl. I; 1909, p. 361, and in systematic section). They emphasized the similarity to pigmentation in birds, pointing out that when salticid males are more conspicuously colored than the females, the young usually resemble the females, and that when the adults are similar, the young resemble them both. The Peckhams were well aware of the gradual development of color, of the appearance of patterns at particular instars and of their probable phylogenetic significance; it is to be regretted that they published no papers devoted to the subject.

Moles (1916, p. 146) briefly described the color of young *Phidippus* sp., probably of the second instar, in California.

It remained for Bonnet (1933, pp. 132-133) to describe and figure the color patterns of the carapace and abdomen of a salticid, *Philaeus chrysope*, during all the instars. As with the Venezuelan species, the first instar after hatching (the *stade nymphal*) has a pale abdomen (yellow in this species). The second instar, also passed entirely within the cocoon, is metallic blackish-green all over; from the third instar (when the young leave the cocoon) through the penultimate, the sexes are both gray with black spots and bands, showing little change during growth and are roughly similar to the adult female. The black of the carapace increases, however, with succeeding molts, and in adults of both sexes the dorsal black abdominal bands develop into a median, longitudinal stripe. Only in the adult male does vermilion appear on the abdomen.

A few papers may be mentioned which are of particular importance in the study of salticid color development, although they concern it only indirectly:

Simon (1901) gave a résumé for each salticid subfamily of the general color characteristics in the various genera, while Di Caporiacco (1940) emphasized the importance of recording color variations in spider systematics because of their frequent genetic basis.

Apparently no work has been done from a biochemical point of view on the development of pigment in young salticids, although Millot's classic study of the histology of spiders in general gives an excellent basis for future work. He found (1926, p. 99) that the integumentary pigments are of four types, all excretory: guanin, responsible for white; melanin, for black, gray and dark brown; the caratinoids, which form yellow, orange and red; and a green pigment of undetermined affinities. Salticids are not mentioned specifically in his discussion of pigments, but he included three species of that family in his list of histological material. Although he was speaking specifically of hypodermal and subhypodermal pigments of adults, visible through the translucent cuticle, the same excretory origin must hold for the superficial colored elements — hairs, scales and intermediate structures—which, along with the cuticle itself, also originate in the hypodermis, and are very prevalent in salticids of all ages.

As Millot points out, the hypodermal colors are not shed during ecdysis, and hence can be accumulated during life. Judging by their hues, these are principally melanins in salticids, with occasional deposits of guanin in the abdomen. It seems important, however, to emphasize a self-evident corollary which must apply in this family: since the colors of the elements are unchanged between molts (except perhaps through fading), and, indeed, are as superficial as are the scales of Lepidoptera, they are the result of chemical

processes which took place in the preceding instar from that in which they occur as external characteristics of the species. This is similar to the situation in many insects. For example, in pierid butterflies, pterine compounds, which are structurally similar to uric acid and generally regarded as excretory, are deposited in the wing scales during metamorphosis (Wigglesworth, 1939, p. 33 and ref.; Imms, 1948, p. 11 and ref.).

For the eventual understanding of arachnid coloration, we shall need to know the conditions necessary for pigment deposition. It has been found in insects that melanin is often laid down near areas of high metabolism, while guanin deposits are made in regions of low activity (Wigglesworth, 1939, pp. 333, 334). Hormones in insects and other invertebrates are known to be responsible for many color phenomena (Hanström, 1939, and ref.), just as in higher animals. Similar controlling factors unquestionably operate in these spiders.

SYSTEMATIC ACCOUNT.

LYSSOMANINAE.

Lyssomanes bradypilus Crane (1949.1, p. 31).

Adults and Young: The three principal divisions of *Lyssomanes* pigmentation are the translucent green of the integument so characteristic of the genus, the black sub-integumentary markings, and the white, yellow and orange-red superficial elements of the anterior carapace. Sexual dimorphism is slight.

In *L. bradypilus*, from Rancho Grande, the green appears in pale form during the second instar, after emergence from the cocoon; in *L. beebei*, from British Guiana, it appears in the first instar according to Beebe (Crane, 1943, p. 126). The AME, however, acquire their first green a little later, at the end of the second instar. Immature *Lyssomanes* are often more yellowish than adults. In the latter, the green shows no regular sexual dimorphism, but individual variation in the tint is great.

Deep-lying black markings occur frequently in the genus, especially on the appendages, the dorsum and, more rarely, the carapace. In *bradypilus*, they are highly variable, sometimes absent, never appear before the adult stadium, and develop only several days after the molt. The male has from one to four pairs of abdominal spots; females may have one or two pairs, in addition to some markings on the legs. The spots are fugitive in alcohol. In species from other localities, e.g. *nigropictus* Peckham, 1888, the spots are more numerous and relatively constant (Crane, *ibid*).

The colored elements of the anterior carapace develop during the middle instars, when the spider is about half grown and measures about 2 mm. in total length. At this time pale yellow patches appear on the inner (dorsal) sides of the dorsal eye tubercles, especially beside the ALE, while white hairs circle the AME and form a scanty clypeal

band. The penultimate instars are similar except that both dorsal and clypeal scales are more plentiful; the dorsal groups may be mixed with white and show traces of orange-red on inner sides of the ALE tubercles. Adult females sometimes differ from penultimates in the addition of an orange-red crest behind AME; the adult male lacks this crest but has the white clypeal band replaced by orange-red.

In summary, the integumentary green of *Lyssomanes* develops in the earliest stages. Black subintegumentary markings are highly variable and appear, if at all, after the final molt; both sexes may have spots in the abdomen, females only in the legs. Colored elements appear in midgrowth, being yellow around the dorsal eyes and white on the clypeus; the sexes remain similar until the adult stage, when the clypeal band of the male is orange-red while the female may develop a crest of the same hue.

Material: First instar: 40 individuals (2 broods); second instar, 15 (same broods); middle instars, 5; penultimate males, 3; penultimate females, 3.

MARPISSINAE.

Menemerus bivittatus (Dufour).

Ref. to Color Descriptions: *Attus manni* Peckham, 1883, p. 27 (male only). *Menemerus melanognathus*, Peckham, 1888, p. 83 (male only). *Menemerus bivittatus*, Simon, 1901, p. 603; Petrunkevitch, 1925, p. 241. *Marpissa melanognatha*, Peckham, 1909, p. 483. *Marpissa bivittatus*, Comstock, 1940 ed., p. 686.

Adults: Color at Rancho Grande in both sexes characterized by white, gray, light rufous and brown elements which in various proportions cover the dark brown integument above; a strong, narrow, white sub-marginal band present on sides of carapace; large eyes rimmed with rufous scales; leg integument not deeply pigmented, well haired and scaled. Iridescence, the purer hues and strong blacks lacking. Sexual dimorphism moderate, best shown in the following regions: clypeus in male with a strong white band which in female is dull rufous (formed of light rufous and dull white elements). Subproximal chelicera band of white present in male only. Elements of carapace above much darker in male than female, except in central region; integument of appendages also darker in male, especially palp and first leg; other legs distinctly banded; although white appendage hairs are plentiful in both sexes, they are longer and more numerous in female, forming long fringes on anterior and posterior palp margins. Dorsum of male with a broad, median dark brown stripe flanked by grayish-white, the sides being brownish; female dorsum much lighter with a variegated pattern of white, gray and buff hairs, including some irregular and variable chevrons. Light hairs occur plentifully in both sexes on ventral surface. In brief, the male is distinguished by a white

rather than rufous clypeus, darker carapace and legs and a dark stripe on the dorsum, while the female has white-fringed palps and plentiful white elements on carapace and legs.

First Instar: Carapace and abdomen slate gray. Abdomen with basal median dark stripe and, in posterior half, a median light streak flanked by a pair of light blotches. Legs translucent and colorless.

Second Instar: Resemblance to adult female pronounced. Dorsal surface, including ocular quadrangle, median thoracic region and dorsum covered with close-set buffy-brown elements. The effect is formed of grayish-white and rufous elements. Abdomen with a pair of thin, weak, dark stripes, hardly visible, and some barely indicated chevrons. Integument dark brown. Sides of carapace and abdomen covered with rufous scales. Eyes all dark brown, rimmed with rufous scales, except dorsal part of AME which have whitish hairs. Clypeus and mouth-parts scaleless, dark brown. Integument of all palps and legs translucent and colorless except for faint bands on joints from patella distally. Palps plentifully clothed with white hair, but without the pronounced marginal fringes of adult female; legs similarly clothed to a lesser extent, their hairs quite short. Sternum black; venter translucent grayish with very sparse, light hairs.

This second instar differs from adult females as follows: white submarginal carapace band absent; sides of carapace and abdomen more rufous, not dark brown; dorsal elements paler and more homogeneous; clypeus naked, although a few rufous hairs are present on cheeks; palps and legs mostly unpigmented; sternum and venter hairier.

Pre-pre-penultimate Instar, Male: (Probably *Fifth Instar*): Carapace length 2.02 mm. By this stadium the clypeus has rufous elements well developed, but still lacks white. Submarginal white carapace band fully developed. There are no other changes of note.

Pre-penultimate Instar, Male: No change from preceding.

Penultimate Instar, Male: Differs noticeably from adult female only in lack of white palpal fringes and in relatively few white leg hairs.

Penultimate Instar, Female: White palpal fringes and hairs on legs still underdeveloped.

In summary, there is a close resemblance to the adult female even in the second instar; the white submarginal carapace band and rufous clypeal hairs probably appear in the third or fourth instar; white clypeal hairs do not mingle with the rufous until the penultimate male instar. The characteristic pure white clypeal band, dark legs and dark abdominal stripe of the male, and the white palpal fringes of the female, appear only in the final instar.

Comparison with published color descriptions indicate that Florida specimens are more rufous than adult tropical forms; young Rancho Grande specimens show more

rufous elements than the browner and grayer adults. These general scale and hair colorings and a white submarginal carapace band are characteristic of the genus (Simon, 1901, p. 603).

Material: 1st instar: 10 (2 broods); 2nd instar: 14 (1 brood); pre-pre-penultimate instar, male, 3; pre-penultimate instar, male, 3; penultimate instar, male, 3, female, 4.

SYNAGELINAE.

Semorina brachyhelyne Crane (1949.1, p. 35).

Adults: General color brown, scaleless, nearly hairless except for fine hairs on abdomen and a few on appendages; the elongated first legs are darker than the very pale remainder in both sexes. Eyes brown, shifting to black, rimmed scantily with yellow hairs. Sexual dimorphism moderate: in male, palps and first legs much darker than in female; two spots of flat-lying silvery-white hairs on abdomen. In female, general color paler brown, slightly yellowish; tibia and tarsus of palps dorsally with silvery-white hairs; abdominal markings a dark stripe with several dark cross-bars.

First Instar: Pigment lacking.

Penultimate Instar, Male: Paler than adult; first legs scarcely darker than remainder, except for anterior (inner) surface of femur which has pigment strongly developed; white abdominal spots present, but inconspicuous.

Material: First instar, 3 (1 brood); penultimate males, 2.

DENDRYPHANTINAE.

Ashtabula furcillata Crane (1949.1, p. 39).

Adults: Carapace and abdomen above covered with iridescent green scales; a white stripe around sides of carapace and around abdomen; AME rimmed with yellowish scales; first legs dark, remainder pale.

Sexual dimorphism slight: male palps black, female pale greenish-yellow; first legs and sides of carapace black in male, brown in female.

Penultimate Instar, Male: Similar to adult male, but palps greenish-yellow and first legs brown, as in female. Dorsal scales iridescent greenish-bronze, that is, less green than in adult. Abdomen laterally with a dark brown stripe below the usual white stripe of the adult; below this is an iridescent greenish stripe extending partly on venter, as in adult. Sternum and venter brown.

Penultimate Instar, Female: Entire upper surface, carapace and abdomen, covered closely with bluish-gray, non-iridescent scales, bounded laterally from ALE to spinnerets by the usual white stripe of the adult. Clypeus and sides of carapace naked brown. Carapace with a narrow submarginal white border of scales. AME chestnut. Eyes all rimmed completely with white, not yellow. Chelicerae and sternum light brown. Palps pale lemon yellow. Legs entirely translucent

horn, the first legs darker brown like sides of carapace, the first femur anteriorly almost black. A white spot above spinnerets at base. Underside of abdomen almost black with some gray hairs laterally.

Material: Penultimate instar, male, 2, female, 1.

***Sassacus flavicinctus* Crane (1949.1, p. 41).**

Adult Male: Integument black with lemon yellow elements as follows: on carapace, in a pair of dorso-lateral, converging stripes below eyes, a submarginal band and a clypeal band and, on abdomen, a subbasal band, two pairs of dorso-lateral bands and, sometimes, a subdistal spot. Abdomen otherwise covered with black elements. Front eyes rimmed with rufous elements. Integument of legs black in proximal segments, paler and banded distally, the first leg darker; variable yellow and white hairs and scales on proximal segments anteriorly. Sternum and venter with white hairs.

Adult Female: Sexual dimorphism extreme. General color brown with obscure markings of ochraceous, not lemon yellow: Carapace integument black covered with close-set, monotone, ochraceous brown elements absent only in middle of ocular quadrangle; palps dark with dull yellow hairs; integument of legs banded; dorsum covered with ochraceous brown elements with a reticulated pattern of lighter ochraceous, including a subbasal band.

First Instar: Carapace gray, darkening with age. Coxa, trochanter and femur of all legs dark gray, other segments translucent and colorless; abdomen pale greenish-yellow to grayish-green.

Second Instar: Integument of carapace and abdomen black, completely covered above with a moderately close sprinkling of grayish or greenish-white short hairs. Large eyes rimmed with similar hairs. Integument of legs all conspicuously banded light and dark.

Pre-penultimate Instar, Male: Like adult male, the lemon yellow markings being well developed except that those on carapace are paler and narrower; second pair of abdominal bands may meet in midline; no subdistal abdominal spot; dark scales in middle of dorsum brown, not black; patches of light hairs on legs at distal tips of second, third and fourth femora only. Hairs on underside scanty but in typical arrangement.

Penultimate Instar, Male: Lemon yellow carapace markings now of adult width and intensity, but legs and abdomen as in preceding stage.

Penultimate Instar, Female: Differs from adult in presence of a definite carapace band of ochraceous or light brown scales among the dark brown elements, passing below ocular quadrangle and behind it across thorax. Abdominal reticulations more obscure than in adult.

Material: 1st instar, 15 (2 broods); 2nd, 10 (2 broods); pre-penultimate male, 1; penultimate male, 3; penultimate female, 2.

***Sassacus ocellatus* Crane (1949.1, p. 34).**

Adults: In both sexes, integument of carapace and abdomen black covered above with iridescent green scales, with a pair of black spots, each crossed by a white bar, near tip of abdomen; clypeus white; second, third and fourth legs brown.

Sexual dimorphism slight: a submarginal white carapace band present in female only, and her face with more white elements; integument of palps and first legs black in male; palps banded in female, and first legs brown, except for black femur; white scales on distal segments of legs in male only; a subbasal pale abdominal band in female only.

First Instar: Carapace dark gray; abdomen pale green; legs translucent and colorless.

Penultimate Instar, Male and Female: Differs from adult as follows: iridescence less well developed, bronze green rather than emerald; palps pale except for darker femur; first legs paler than adult and all other legs well banded at joints, not uniform brown; a few yellowish-white scales on first leg only, anteriorly only; a narrow white submarginal carapace band as in female; a subbasal abdominal band extending well along sides, also as in female; above this, in the black, non-iridescent stripe, are three pairs of white, dorso-lateral cross-bars, the first two very faint, the most posterior strong and persisting in the adult.

Material: First instar 6 (1 brood); penultimate instar, males 4, female 1.

HYLLINAE.

Phiale spp.

The *Phiale* of the Rancho Grande region include at least three species, of which one, from Rancho Grande itself, has been described as new (*P. flammea* Crane, 1949.1, p. 47). *P. dybowskii* (Taczanowski, 1871) occurs at somewhat lower altitudes; in color it checks perfectly with Chickering's description (1948, p. 217). A third species is highly variable and remains undescribed for lack of an adequate series; it is fairly common and overlaps the ranges of both *flammea* and *dybowskii*. Young of most stadia of presumably all three forms are taken plentifully in June, July and August, but because of their great individual variation, the presence of the poorly defined third species and the essential similarity of the young, it was found impossible to identify the latter without rearing them to the adult. Time limitations prevented this except for several pre-penultimate instars in each species, the first two instars of *flammea* and the first four of *dybowskii*. The male probably passes through seven to eight stadia, depending on the species. The young are relatively easy to rear, and would form an excellent subject for intra-generic comparison studies. Since the course of color development is so similar, it will be sketched below in general terms; the crucial specific differences generally emerge only in the final instar.

Adults: Carapace integument black with a submarginal band of white or creamy scales extending from near pedicel completely around clypeus; above with more or less black or rusty scales and with a median white stripe and/or spots. Abdomen covered with scales ranging from rusty black to brilliant flame scarlet with a subbasal white band extending halfway along sides; a white cross-bar present at least underneath scales; one or more white distal spots usually apparent.

Sexual dimorphism moderate. White or cream carapace bands all more extensive in male than in female, while the remainder of the carapace scales tend to be black, not brown or rusty. Anterior eyes rimmed with rufous in male, with paler in female; palps and at least first legs spotted with white elements in male, paler with few or no white elements in female. Scales of abdomen redder in male than in female, in which it is often more brown than rufous and sometimes practically black; white abdominal markings tend to be overlaid in the male by the rufous scales, particularly in *flammea*. Distal white spots always larger and more conspicuous in female.

First Instar (*P. dybowskii* and *P. flammea*): Carapace gray; abdomen greenish-yellow to olive green; appendages translucent and colorless.

Second Instar (*P. dybowskii* and *P. flammea*): Carapace and abdomen jet black, scaleless, short black hairs scattered on ocular quadrangle and abdomen. AME and ALE surrounded completely by a scanty fringe of relatively long hairs, white around lower AME and all ALE, light rusty around upper half of AME. All eyes jet black. Chelicerae black. Black pigment present at least proximally at least in palp and first leg in both species; banding may occur in third and fourth legs in *flammea*, markings longitudinal in *dybowskii*.

Third Instar (*P. dybowskii*): Differs from second in presence of two pairs of short, lateral, white abdominal bars, one toward middle of length and one behind; a few rusty hairs across middle of abdomen; a faint median pale abdominal spot; ocular quadrangle with a scanty covering of dull brown scales.

Fourth Instar (*P. dybowskii*): Differs from third in bronze sheen of ocular quadrangle scales, in presence of a short, slender, subbasal white abdominal band; two pairs of lateral white bars of the third instar are now only spots; median spot now extended as a broad, faint cross-bar, the central spot remaining strong. No white on clypeus; rust around anterior eyes present; slightly more black pigment on legs.

Pre-penultimate Instar, Males and Females, All Species: Carapace scalation now about as well developed as in adult females, including white band and clypeal hairs. Legs still with less black pigment than in adult and few or no white scales. Abdomen black, only

tinged with rufous, the white bands strongly edged with black.

Penultimate Instar, Males and Females, All Species: Similar to adult females, but fine specific color distinctions, such as the terminal hooks on the subbasal abdominal band of *dybowskii*, are not yet developed. White palp and leg scales less numerous than in adult females.

Material: *P. dybowskii*: first instar, 10; second, 10; third, 4; fourth, 3; all first four instars from a single brood; pre-penultimate instar, male, 1, female, 1; penultimate instar, male, 3, female, 2. *P. flammea*: first instar, 15 (3 broods); second instar, 10 (4 broods); pre-penultimate instar, males, 2, females, 3; penultimate instar, males, 4, females, 4. *Phiale* spp.: Pre-penultimate and penultimate instars, males and females, records made of pattern variations only, 19 (not all reared to adult).

PLEXIPPINAE.

Corythalia spp.

The development of color and pattern in three species of Rancho Grande *Corythalia* has already been traced in detail (Crane, 1948, pp. 15-17, 24-25, 29-33; general résumé on pp. 3 ff. and Text-fig. 2.

The following *errata* should be noted in that publication: In the figures and descriptions of the stadia of *C. xanthopa* it was assumed that there were 7 male and 8 female instars, as in *C. chalcea* and *fulgipedia*, although *xanthopa* had not been reared throughout its cycle. During a subsequent season at Rancho Grande, examples of both sexes completed development from egg to adult. There proved to be only 6 male and 7 female instars. (This might have been expected from the smaller size of the adult, although there was an unusually large size increase after the third instar in the earlier material; see *ibid.*, Text-fig. 11). Therefore, no instar was missing after all from the published series, and the following corrections should be made concerning the *xanthopa* color descriptions: Text-fig. 2 (opp. p. 4): T - X, incl., actually represent the 4th, 5th male, 6th female, 7th female (adult) and 6th male (adult), respectively. The correspondence of the instar positions in the three species is, however, unchanged, since the pre-penultimate, penultimate and adult stadia in each species are still comparable, regardless of the number of the instar. Similar shifts, to one instar number lower, should be made in the text on pp. 30, 32 and 33, namely: "Fourth Instar: Unknown" should be eliminated; for "fifth instar" read "fourth," for "sixth" read "fifth" and for "seventh" read "sixth" throughout.

MAGONINAE.

Mago denticelis Crane (1949.1, p. 49).

Adults: In both sexes, carapace integument black with a median stripe of white scales enclosing a central black spot. Sparse chestnut and black hairs around and near

eyes. Abdomen covered with brown, mixed with gray and white, scales in a variable, somewhat lyre-shaped, whitish marking, including a subbasal band; a pair of subdistal spots.

Sexual dimorphism slight. Palps black in male, pale in female; first two legs except tarsi black in male, other legs banded, whereas all legs are banded in female; white elements present on appendages in male, scanty or absent in female; posterior abdominal spots more distinct and constant in male.

First Instar: Carapace and legs translucent white; abdomen pale translucent yellow with three pairs of irregular, dark gray, dorsal blotches and a fourth pair, at extreme base, running laterally. The most distal pair join across the abdomen as a bar.

Second Instar: Carapace, abdomen and legs all pale translucent buff with strong black markings. Ocular quadrangle with a thin frosting of coarse yellow hairs, especially around all eyes including front. Immediately behind each posterior eye is a curved spot and a pair of curved bars on either side of midline at same level. Midway down thoracic slope a pair of shorter curved bars and on mid-side of carapace, just behind eye level, a long horizontal bar; carapace is bordered narrowly with black from level of first leg to just before pedicel. Face and chelicerae naked and translucent (except around eyes) as are palps except for black tip of femur and all patella. Sternum translucent. All legs strongly banded with black at joints except coxae and trochanters, the latter having a single spot.

Abdomen with a pair of basal dark spots, then a narrow cross-bar, interrupted in middle, followed by a midline group of irregular spots, though posteriorly there are two larger ones; this group is just behind high point of abdomen. Behind this is a pair of L-shaped markings, then a narrow cross-bar, convex anteriorly, the median part preceded by a still narrower, almost contiguous bar. Finally a pair of terminal black spots, touching spinnerets. Some long hairs all over abdomen and legs. Venter with some white, flat-lying hairs.

Penultimate Instar, Male: Differs from adult in relative inconspicuousness of the abdominal lyre-shaped pattern. The dominant markings, instead, are three pairs of small pale buff spots, in posterior half of abdomen.

Material: First instar, 13 (2 broods); second, 7 (1 brood); penultimate male, 1.

SUMMARY AND CONCLUSIONS.

A brief general survey of salticid color development will now be made, based on the juvenile and adult material of the eleven species specially treated in this and preceding papers of the series. These species were selected as characteristic of their respective subfamilies and are widely distributed systematically throughout the family; they illustrate the principal characteristics of salticid coloration and sexual dimorphism.

The regions of the body will be considered in turn. As usual, a distinction will be maintained between the colors of the integument and that of the colored elements, the hairs and scales, which overlie them. Often these elements are in sharp contrast to the generally dark integument, and the distinction is valid. Sometimes, however, the two structures bear a close color relation to each other. For example, female palps may have both pale integument and long white fringes, as in *Menemerus* and *Semorina*. Again, generically constant pale abdominal bands appear hypodermally in *Corythalia* in the scaleless first instar, and are later covered by corresponding bands of light-colored scales.

Integument: Carapace and abdomen nearly or quite colorless on hatching, but hypodermal pigment, visible as dull gray or green, develops toward the end of the stadium. When the spider is very black in adults of both sexes, the carapace is completely black in the second instar; this is true in *Sassacus* (Dendryphantinae), *Phiale* (Hyllinae) and *Corythalia* (Plexippinae). In others, where the adult is brown, or black only in the male, it darkens gradually, as in *Mago denticchelis* and an undescribed species of *Hypaeus* (both Magoninae).

The appendages develop pigment more slowly, even those that are completely black in the adult. They are sometimes quite colorless up to the middle instars; usually they are pigmented proximally or lightly banded at the joints, as early as the second.

Special patches of iridescent integument, as on the chelicerae of some dendryphantinids or the legs of *Corythalia*, appear only in the adult male.

Hairs, Scales and Intermediate Elements: These are conveniently divided into eleven rather well defined areas which appear throughout the salticids, regardless of subfamily.

1. Circumorbital markings: Along with the hairs of the dorsum, these are the most universally present and earliest-appearing of the colored elements. They appear around the AME and sometimes other eyes in the second instar, in all species studied except *Lyssomanes*; in the latter they develop later. When they first appear they are white, light yellow or rufous; in adults they range from orange to rufous. They are little variable intraspecifically, although they are sometimes brighter in males, as in *Phiale*.

2. Postorbital crest: Rare; white to orange-red; appears in adult only, male or female. When present, of variable length and thickness. Examples: *Lyssomanes bradyspilus*; *Hypaeus* sp. (undescribed).

3. Dorsal carapace: Including ocular quadrangle, region immediately below it, and thoracic region. Very variable within every species in adults, the female usually hairier or scallier than the male; in fact, these regions are sometimes more nearly naked in the adult male than in the penultimate. The elements may appear as a dense covering in

the second instar or, more usually, not before the third. Although all colors may be present, white stripes or spots are most frequent among striking dorsal markings at all ages (Examples: *Phiale*; *Corythalia fulgipedia*; *Mago denticheleis*). Sometimes (*Sassacus flavicinctus*) paired stripes appear as a secondary sexual character in the male, although they are indicated in the penultimate female.

4. Submarginal carapace band: Very common, as in many other families. White, cream or yellow; wide or narrow; sexual dimorphism various; better developed in adult male *Phiale* than in female, but secondarily lost in adult male *Sassacus ocellatus*; or dimorphism may be negligible as in *Corythalia fulgipedia*. May show considerable individual variation or practically none. Appears in third instar or later.

5. Clypeal band: Extremely common. Any color or mixture, but most common form is a strong white band which is strongly developed only in adult male (example: *Menemerus bivittatus*). Female may have an equal number of elements, but they are rarely of a single color and their disposition is not so exact; they often extend up over the cheeks. Elements sometimes secondarily reduced in adult male, giving a practically naked black clypeus, as in *Corythalia chalcea* and *fulgipedia*. Little intraspecific variation. First hairs appear in middle instars.

6. Chelicerae and mouthparts: Usually nearly naked throughout development except for marginal brushes and a few unspecialized hairs; adult male sometimes with a proximal anterior brush of long hair on chelicerae supplementing the clypeal band.

7. Palps: Often show considerable sexual dimorphism in adults. In the female may be pale and fringed with long white hairs (*Menemerus bivittatus*, *Semorina*), while the corresponding male palps are dark and lack fringes. In others, the female palps are medium brown while the males are black with anterior patches of shiny white or yellow scales (*Phiale*; *Corythalia xanthopa*). These extreme examples of sexual dimorphism appear only in the adult. Palps of the young always have some hairs, even in the first instar; later, both dark and light elements are present.

8. Legs: When the first legs of adult males are darker than the others, they are sometimes furnished anteriorly with bands or spots of white scales, as in *Phiale*. Usually they are also present, though fewer, posteriorly and on the other legs. These white scales may be mixed with scales of other colors in females and young, where they may be much more numerous, but not in the contrasting pattern of the male. The female too may have fewer pale leg scales than during earlier instars, as in *Corythalia fulgipedia*. In some species striking fringes appear abruptly in adult males, on legs active in display (*Corythalia* spp.). General hairiness, highly variable individually, is a usual growth character, appearing even in the first

instar; the hairs usually become darker with succeeding stadia.

9. Sternum: Usually not very hairy, and the hairs are unspecialized, being short but not scaly, ranging from pale to black, and increasing in number from the earliest instars.

10. Dorsum: A few long hairs present in first instar; bands or spots or a general covering characteristic of the genus sometimes present in the second, formed of a few relatively large scales (*Corythalia*; *Sassacus*). By the middle instars, if not before, the dorsum is completely covered with elements ranging from hairs to full scales. Various chevron-like patterns, which prevail so widely in spiders, may be present, particularly in the young (as in *Menemerus bivittatus*). Details of the dorsal pattern are often highly variable after the middle instars. Iridescence appears in mid-growth in species of which it is a characteristic, and develops gradually; sometimes, as in *Ashtabula furellata*, the iridescent covering of the dorsum may be continuous with that of the upper part of the carapace. In the same species is illustrated the occasional continuation of the submarginal carapace band down the length of the abdomen. A pale subbasal abdominal band is found widely throughout the family, at least in females (examples: *Sassacus*, *Phiale*, *Corythalia*, *Mago denticheleis*); in *Corythalia* it appears in the second instar; in the other forms it develops later.

11. Venter: Usually hairier than sternum; a drab pattern, often involving longitudinal stripes, is usually present from an early instar.

* * *

In brief, the first pigments to develop are the hypodermal melanins of eyes, carapace and abdomen, along with variously colored hairs and scales, chiefly circumorbital and abdominal. The white submarginal carapace band, if any, appears fairly early, as does the subbasal abdominal band. The hypodermal melanin of the appendages is deposited gradually throughout the instars, and is usually most intense in the chelicerae, palps and first legs of adult males. White hairs and scales on carapace and legs sometimes are most numerous in both sexes in the penultimate instar, being secondarily reduced at least in the adult male. Iridescent scales develop gradually in the middle instars, but reach maximum development only in the adult, usually in the male. Last to appear are many sexually dimorphic specializations, such as shiny white clypeal bands and palpal patches of specialized scales and scale hairs, cephalic crests, appendage fringes, areas of intense yellow, orange or scarlet scales, and secondarily naked patches of iridescent cuticle.

Because of the late appearance of these specializations, sexual dimorphism of pattern and color is usually not apparent before the penultimate instar of the male and often not until after the final male molt.

It is obvious, as pointed out years ago by the Peckhams, that this general course of color development parallels that of many animal groups, for example birds and fishes, in addition to that of spiders as a whole. There is the usual gradual increase in pigment, the young frequently resemble the adult female and there is often a striking change in the adult male consisting of the appearance of more intense and more contrasting pigmentary or structural colors.

Of special interest in this comparative study of a family are the clues to phylogenetic relationships, to be considered in a subsequent paper. As stated above, the order of development of the various components and areas of color are similar, regardless of the phylogenetic position of the genus or subfamily. It seems apparent, however, that juvenile pigment patterns, as well as the time of their appearance and the variability of the pattern elements, furnish some hints of species relationships within a genus, which are useful when used in connection with other evidence. At present they are of little help in tracing affinities in higher categories. When up-to-date studies, both chemical and genetic, can be made of the pigments at various instars in the various species, the usefulness of pattern and color in tracing phylogeny will doubtless be extended.

REFERENCES.

- BEEBE, W., & CRANE, J.
1947. Ecology of Rancho Grande, a subtropical cloud forest in northern Venezuela. *Zoologica*, Vol. 32, No. 5, pp. 43-60.
- BONNET, P.
1933. Cycle vital de *Philaeus chrysops* Poda. *Arch. Zool. Expér.*, Vol. 75, pp. 129-700.
- CAPORACCO, L. DI
1940. Il valore delle variazioni di colorazione negli Aracnidi. *Redia*, Vol. 26, pp. 221-237.
- CHICKERING, A. M.
1946. The Salticidae (Spiders) of Panama. *Bull. Mus. Comp. Zool., Harvard Coll.*, Vol. 97.
- COMSTOCK, J. H.
1940. The spider book. Doubleday, Doran & Co., N. Y. 1940 ed. revised & ed. by W. J. Gertsch.
- CRANE, J.
1943. Spiders of the families Lyssomanidae and Salticidae (Magoninae) from British Guiana and Venezuela. *Zoologica*, Vol. 28, pp. 125-138.
1948.1. Comparative biology of salticid spiders at Rancho Grande, Venezuela. Part I. Systematics and life histories in *Corythalia*. *Zoologica*, Vol. 33, pp. 1-38.
1948.2. Comparative biology of salticid spiders at Rancho Grande, Venezuela. Part II. Methods of collection, culture, observation and experiment. *Zoologica*, Vol. 33, pp. 139-145.
1949.1. Comparative biology of salticid spiders at Rancho Grande, Venezuela. Part III. Systematics and behavior in representative new species. *Zoologica*, Vol. 34, pp. 31-52.
1949.2. Comparative biology of salticid spiders at Rancho Grande, Venezuela. Part IV. An analysis of display. *Zoologica*, Vol. 34, pp. 159-214.
- HÄNSTROM, B.
1939. Hormones in invertebrates. Oxford University Press, New York, ix + 198 pp.
- HOLM, A.
1941. Studien über die Entwicklung und Entwicklungsbiologie der Spinnen. *Zoologiska bidrag från Uppsala*, Vol. 19, pp. 1-214.
- IMMS, A. D.
1948. A general textbook of entomology. Seventh edition. E. P. Dutton & Co., New York.
- MILLOT, J.
1926. Contribution a l'histophysiologie des Araneides. *Bull. Biol. France et Belgique*, Suppl. 8, pp. 1-238.
- MOLES, M. L.
1916. Growth and color patterns in spiders. *Jour. Entom. & Zool. Pomona Coll.*, Claremont, California, Vol. 8, pp. 129-150.
- PECKHAM, G. W. and E. G.
1888. Attidae of North America. *Trans. Wisc. Acad. Sci. Arts Let.*, Vol. 7, pp. 1-104.
1889. Observations on sexual selection in spiders of the family Attidae. *Occ. Papers Nat. Hist. Soc. Wisconsin*, Vol. 1, pp. 3-60.
1909. Revision of the Attidae of North America. *Trans. Wisc. Acad. Sci. Arts Let.*, Vol. 16, pp. 355-646.
- PETRUNKEVITCH, A.
1925. Arachnida from Panama. *Trans. Conn. Acad. Arts & Sci.*, Vol. 27, pp. 51-248.
- SIMON, E.
1901. Histoire naturelle des Araignées. Vol. II, pp. 381-429.
- TACZANOWSKI, L.
1871. Les Araneides de la Guyane française. *Horae Soc. Entom. Ross.*, Vol. 8, pp. 32-132.
- WAGNER, W.
1888. La mue des Araignées. *Ann. Sci. Nat., Ser. 7 (Zoologie)*, Vol. 6, pp. 280-293.
- WIGGLESWORTH, V. B.
1939. The principles of insect physiology. E. P. Dutton & Co., London, New York. 434 pp.